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ORIGINAL ARTICLE

Adolescent male chimpanzees do not form a dominance hierarchy with their peers

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Abstract Dominance hierarchies are a prominent feature of the lives of many primate species. These hierarchies have important fitness consequences, as high rank is often positively correlated with reproduction. Although adult male chimpanzees strive for status to gain fitness benefits, the development of dominance relationships is not well understood. While two prior studies found that adolescent males do not display dominance relationships with peers, additional research at Ngogo in Kibale National Park, Uganda, indicates that adolescents there form a linear dominance hierarchy. These conflicting findings could reflect different patterns of rank acquisition across sites. An alternate possibility arises from a recent re-evaluation of age estimates at Ngogo and suggests that the report describing decided dominance relationships between adolescent males may have been due to the accidental inclusion of young adult males in the sample. To investigate these issues, we conducted a study of 23 adolescent male chimpanzees of known age during 12 months at Ngogo. Adolescent male chimpanzees exchanged pant grunts, a formal signal of submission, only 21 times. Recipients of pant grunts were late adolescent males, ranging between 14 and 16 years old. In contrast, younger adolescent males never received pant grunts from other males. Aggression between adolescent males was also rare. Analysis of pant grunts and aggressive interactions did not produce a linear dominance hierarchy among adolescent males. These data indicate that adolescent male chimpanzees do not form decided dominance relationships with their peers and are consistent with the hypothesis that the hierarchy described previously at Ngogo resulted from inaccurate age estimates of male chimpanzees. Because dominance relationships develop before adulthood in other primates, our finding that adolescent male chimpanzees do not do so is surprising. We offer possible explanations for why this is the case and suggest future studies that may help clarify the matter.

Keywords Rank · Adolescence · Aggression · Development · *Pan troglodytes*

Introduction

Many social animals, including primates, form dominance hierarchies (Bernstein 1976). Some of the best information regarding dominance relationships derives from studies of Old World monkeys (subfamily Cercopithecinae, Altmann 1962; Samuels et al. 1987). Here adult male and adult female cercopithecine monkeys establish separate dominance hierarchies (Koford 1963; Seyfarth 1976; Hausfater et al. 1982). For males, competition for rank can be especially intense (Gesquiere et al. 2011) because high rank confers fitness benefits. In several primate species, high-ranking males reproduce more than do low-ranking males (Alberts 2012).

Given the important fitness consequences of high rank for adult primates, considerable attention has been given to its development. Studies of cercopithecine monkeys, including baboons and macaques, reveal that dominance relationships form early during development in both females and males (Koyama 1967; Cheney 1977; Johnson

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1987; Pereira 1988, 1989, 1995). Female baboons and macaques remain in their natal communities for life. As juveniles, they acquire and maintain ranks adjacent to their kin with the help of their mothers and maternal relatives (Cheney 1977; Lee and Oliver 1979; Berman 1980; Horrocks and Hunte 1983; Chapais 1988; Datta 1988). Like their sisters, juvenile and adolescent male baboons and macaques also obtain support from their mothers before they disperse to new groups. However, in contrast to females, a male's size and age are often better predictors of his dominance rank than is his mothers' rank (Koford 1963; Johnson 1987; Pereira 1989). While still living in their natal groups as juveniles and adolescents, male baboons and macaques display aggression to peers, using competitive asymmetries due to size and age to dominate others (Lee and Oliver 1979; Johnson 1987; Pereira 1995).

Studies of adult male chimpanzees have shown that they too strive for status, forming dominance hierarchies in the process (Bygott 1979; Goodall 1986; Newton-Fisher 2004; Mitani 2009). As adults, male chimpanzees acquire their dominance rank using aggression and coalitionary behavior (Nishida 1983; Goodall 1986; Hayaki et al. 1989; Nishida and Hosaka 1996; Muller and Wrangham 2004a, b). Once established, male chimpanzee dominance relationships are commonly acknowledged by a call, the pant grunt. Pant grunts are formal signals of submission and are always directed up the hierarchy, given unidirectionally by a subordinate chimpanzee to a dominant one (Bygott 1979; Noë et al. 1980; De Waal 1982). Adult male chimpanzees compete vigorously with each other because, as is the case with cercopithecine monkeys, high status confers reproductive benefits. High-ranking males typically produce more offspring than do low-ranking males (Boesch et al. 2006; Duffy et al. 2007; Wroblewski et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2013). Despite the importance of dominance relationships for adult male chimpanzees, scant information exists about its development.

Male chimpanzees take a long time to grow up. As they do so, they remain in their natal groups. For the first 8 to 10 years of their lives, male chimpanzees travel almost constantly with their mothers (Pusey 1983, 1990), joining and leaving other community members throughout the day in the fission–fusion pattern characteristic of chimpanzees (Nishida 1968; Goodall 1983). As infants and juveniles, chimpanzees interact with other community members, but these interactions are largely influenced by the social relationships and status of their mothers (Lonsdorf et al. 2014; Murray et al. 2014). Infants begin to give pant grunts to adults during their first few months of life. While still being carried ventrally by their mothers, they will sometimes pant grunt in tandem with their mothers as they approach a high-ranking male (Nishida 2012). Juvenile and adolescent chimpanzees also give pant grunts to adult males when greeting them (Pusey 1990).

Male chimpanzees start to become socially independent during adolescence (Pusey 1983, 1990; Goodall 1986). Although mothers and sons can maintain life-long social bonds, they travel less often together when males reach adolescence. By age 12 or 13, adolescent males predominantly follow adult males throughout the territory or travel alone (Pusey 1983, 1990; Hayaki 1988; Kawanaka 1989). Between this time and adulthood, adolescent males' dominance relationships with adult community members change drastically. At the start of adolescence, male chimpanzees are small and are unable to dominate adult females. During this time, they are especially submissive to adult males. By the end of adolescence, males appear to have reached adult height (Sandel, unpublished data) but continue to increase in body weight (Pusey et al. 2005). At this point, they are able to dominate all community females and start to challenge adult males for a position in the adult male hierarchy (Goodall 1986; Muller and Wrangham 2004a). Although these details regarding the social relationships of adolescent and adult male chimpanzees have been well documented, the relationships between adolescent males themselves remain unclear. Specifically, prior studies have produced conflicting findings regarding whether adolescent males establish decided dominance relationships with their peers.

In the first detailed description of dominance relationships between wild male chimpanzees, Bygott (1979) found that subadults at the Gombe National Park did not form a rank hierarchy with each other. He noted: "Although immature males pant-grunted to adult males, they were not seen to pant-grunt to one another" (Bygott 1979: 414). Similarly, Hayaki et al. (1989) found that adolescent males in the Mahale Mountains National Park rarely pant grunted to each other. Pant grunts were also exchanged infrequently between adults. Of the relatively few that were given, most were directed to the alpha male. The paucity of data made it difficult to determine dominance relationships between some adult males, and the dominance relationships between adolescents could not be specified at all (Hayaki et al. 1989). Additional study at Gombe indicated that one 13-year-old adolescent male there behaved aggressively to an adult male, receiving pant grunts from him in the process (Pusey 1990). Nevertheless, dominance relationships between adolescents were not described, and a clear hierarchy involving them did not appear to exist.

In contrast to prior findings from Gombe and Mahale, Sherrow (2012) found that adolescent males at Ngogo in the Kibale National Park establish decided dominance relationships. Sherrow (2012) recorded 99 pant grunts between adolescent males and was able to construct a linear dominance hierarchy involving them. Because the Ngogo chimpanzee community is quite large compared to

other chimpanzee groups, it is possible that demographic conditions created a highly competitive environment, leading adolescent males to form a dominance hierarchy to manage potentially high levels of aggression.

A different explanation for the finding that adolescent males at Ngogo form a dominance hierarchy emerges from analysis of long-term demographic records there and a reconsideration of male ages (Wood et al. 2016). Continuous observations of the Ngogo chimpanzees began in 1995 (Watts 2012). Therefore, when Sherrow started his study in 2000 he lacked information regarding the precise ages of his adolescent male subjects. Instead, as is the case in all other field studies of chimpanzees, male ages were initially estimated. Recently, age estimates of the chimpanzees at Ngogo have been reassessed and refined, using pedigree and genetic data (Wood et al. 2016). Applying these adjusted age estimates to Sherrow's sample indicates that nine of the 17 males he considered adolescents are likely to have been young adults during most of his study (Table 1). Thus, the finding that adolescent males at Ngogo form a dominance hierarchy may have been an artifact of including young adults in the sample.

To address the contradictory findings reported in prior studies regarding adolescent male chimpanzee dominance relationships, we conducted a follow-up study of dominance and aggression between adolescent males at Ngogo in the Kibale National Park, Uganda. We followed adolescent males in the same community of chimpanzees observed earlier by Sherrow (2008, 2012). We collected observations 10 years after Sherrow did, and thus followed an entirely new cohort of adolescent males whose birth dates are known to within 1 month to 1 year. Using this new sample of males allowed us to test the hypothesis that inaccurate age estimates may have created a false impression that clear dominance relationships exist between adolescent males at Ngogo in contrast to other chimpanzee communities.

Methods

Study site and subjects

We conducted observations of adolescent male chimpanzees at Ngogo, Kibale National Park, Uganda, from

Table 1 Male chimpanzees observed in a previous study at Ngogo

Name	Code	Rank[a]	Age category[a]	Age category updated (2003–2004)[b]	Est. DOB[b]	Age Aug 2000[b]	Age Dec 2004[b]
Dexter[c,d]	**DX**	**1**	**Late adolescent**	**Young adult**	1985	15.6	19.9
Getz[c]	**GZ**	**2**	**Late adolescent**	**Young adult**	1986	14.6	18.9
Rahsaan[c]	**RN**	**3**	**Late adolescent**	**Young adult**	1987	13.6	17.9
Webster[c,d]	WB	4	Late adolescent	Late adolescent	1988	12.6	16.9
Tatum[c,d]	**TA**	**5**	**Late adolescent**	**Young adult**	1986	14.6	18.9
Rollins[c]	**RO**	**6**	**Late adolescent**	**Young adult**	1986	14.6	18.9
Branford[c,d]	**BD**	**7**	**Late adolescent**	**Young adult**	1987	13.6	17.9
Richmond[c,d,e]	**RI**	**8**	**Late adolescent**	**Young adult**	1987	13.6	17.9
Carter[c]	CA	9	Mid adolescent	Mid adolescent	1990	10.6	14.9
Mulligan[c]	MU	10	Mid adolescent	Late adolescent	1989	11.6	15.9
Garrett[c,d]	GT	11	Mid adolescent	Late adolescent	1989	11.6	15.9
Waller[c,e]	**WA**	**12**	**Late adolescent**	**(Young) adult**	1982	18.6	22.9
Satchmo[c]	**SA**	**13**	**Early adolescent**	**Young adult**	1987	13.6	17.9
Jackson[f]	JA	14	Early adolescent	Mid adolescent	1991	9.6	13.9
Cash[c]	CS	15	Early adolescent	Early adolescent	1993	7.6	11.9
Southpaw[c]	SP	16	Early adolescent	Early adolescent	1993	7.6	11.9
Herbie[c]	HH	17	Early adolescent	Early adolescent	1994	6.6	10.9

The age class of male subjects and their ranks are shown as reported in Sherrow (2012). Updated age estimates used in this study are also listed. Males whose age estimates are not the same are indicated in bold

[a] Based on Sherrow (2008, 2012)

[b] Based on current consensus among directors of Ngogo Chimpanzee Project (Kevin Langergraber, John Mitani, David Watts); birthdate assigned to the first of January of the estimated year of birth

[c] Estimated based on physical appearance compared to chimpanzees of estimated age at the time and known age retrospectively

[d] Estimated based on older sibling

[e] Estimated based on younger sibling

[f] Estimated based on physical appearance compared to chimpanzees of known age

August 2014 through August 2015. Ngogo lies at the center of the Park and is covered mostly by old growth rainforest interspersed by regenerating forest and grasslands (Struhsaker 1997). The Ngogo chimpanzees have not been provisioned by humans, and their territory is surrounded on all sides by other chimpanzee communities.

The chimpanzees at Ngogo have been observed continuously for 21 years and are habituated to human presence (Mitani 2009). The Ngogo chimpanzee community is extremely large. For most of the study period, it consisted of 193 individuals, including 31 adult males, 23 adolescent males, 63 adult females, 15 adolescent females, 10 juvenile males, 5 juvenile females, and 46 infants. As we conducted this study, some changes in the age-sex class composition of the community occurred due to births, deaths, and immigration.

Our subjects included 11 early adolescents (8–10 years old), 5 middle adolescents (11–13 years old), and 7 late adolescents (14–16 years old). One male (Barron) turned 14 years old during the course of the study and was considered a late adolescent thereafter. These age categories correspond to physical and social milestones in male chimpanzee development and are based on previous studies conducted on chimpanzees at the Gombe National Park, the Mahale Mountains National Park, and Ngogo (Goodall 1983, 1986; Kawanaka 1989; Sherrow 2008). Early adolescents have enlarged testicles relative to juveniles but are about half the size of adults; they spend most of their time traveling with their mother. Middle adolescents are larger than early adolescents, have pronounced testicles, spend variable time with their mothers, and are still growing. Late adolescents are similar in height but slimmer than adult males. Late adolescent males spend a majority of their time away from their mothers. Exactly when male chimpanzees transition from adolescence to adulthood is not easy to discern. In the past, chimpanzee researchers have relied on chronological age to distinguish the two types of males, often considering males older than 15 years to be adults (Goodall 1983, 1986; Boesch and Boesch-Achermann 2000; Nishida et al. 2003; Sugiyama 2004; Reynolds 2005). While age and physical size undoubtedly change in tandem as males mature and make the transition to adulthood, their social behavior also undergoes profound transformation. Unlike adolescent males, adult male chimpanzees are fully integrated into the social network of other adults in the community (Goodall 1986). Because the 15- and 16-year-old males in this study were not well integrated into the social world of prime adult males (Sandel, unpublished data), we considered them to be late adolescents instead of adults. While this age cut-off to demarcate adulthood differs from that used by some other chimpanzee researchers (Muller and Wrangham 2004b; Wroblewski et al. 2009), it is consistent with the one employed in the previous study at Ngogo (Sherrow 2008, 2012), whose results we re-examine in this paper.

In all studies of wild animals, the ages of individuals born before the initiation of continuous long-term observation are estimates. At Ngogo, continuous study of adult males began in 1995. Detailed observations of adult females, who are the mothers of our subjects, were initiated in 2003. Thus, most of our subjects, who were adolescents in 2014, were identified in infancy, and their birth dates are known to within 1 month to 1 year. When the exact date of birth of males was unknown, they were assigned a birthdate on the 1st or 15th of the month, depending on when they were first observed during the month.

Behavioral observations

We collected observations of male pant grunts and aggressive behavior via focal and ad libitum sampling (Altmann 1974). Pant grunts are distinctive and easily recognizable calls that are directed up the dominance hierarchy, given by low-ranking chimpanzees to higher-ranking individuals (Bygott 1979; De Waal and Van Hooff 1981; De Waal 1982). We recorded two types of aggression, contact and non-contact. Contact aggression included hitting, slapping, kicking, and biting. Non-contact aggression included four types of behavior: (1) displays occurred when a male ran within 5 m of another individual. Displaying males were often piloerect and dragged branches behind them; (2) charges involved males running directly toward another individual instead of past them as in displays; (3) chases were recorded when a male ran directly toward another individual and continued to run after victims as they moved away; (4) other forms of agonism constituted a fourth class of non-contact aggression. Behaviors in this category included shaking branches and swatting an arm abruptly at another individual. When non-contact aggression escalated to contact aggression, we scored the aggressive event as contact aggression.

We recorded pant grunts and aggression between chimpanzees as they occurred. Sometimes a chimpanzee would approach a group of others, pant grunting in the process. Other times, an individual might charge into another group of chimpanzees. In both cases, the recipients of pant grunts and aggression are unclear. For purposes of the following analyses, we included only pant grunts and aggression whose targets were unambiguous. Our use of ad libitum observations was predicated on the fact that the behaviors of interest, pant grunts and aggression, are rare yet conspicuous (Hayaki et al. 1989).

We followed chimpanzees from approximately 7:30 a.m.–6:00 p.m. daily. We noted which individuals were visible at approximately 30-min intervals to quantify contact time with chimpanzees from whom pant grunts and

aggression were recorded. If we had seen an individual within 14 min of the 30-min interval, we recorded them as present at that time (e.g., if Booker was observed at 11:37 we recorded him as present at 11:30; if we observed him at 11:46, we recorded him as present at 12:00). Based on contact time with chimpanzees, A.A.S. observed them during 2,300 h, including early adolescents (total hours/individual ± SD: 61 ± 29.7 h), middle adolescents (total hours/individual ± SD: 135.6 ± 65.7 h), and late adolescents (total hours/individual ± SD: 146.8 ± 50.5 h). R.B.R. observed chimpanzees during 800 h, including early adolescents (total hours/individual ± SD: 25.6 ± 11.8 h), middle adolescents (total hours/individual ± SD: 49.2 ± 23.2 h), and late adolescents (total hours/individual ± SD: 42.9 ± 14.7 h).

Data collected via ad libitum sampling were supplemented with additional observations recorded during focal animal sampling (Altmann 1974). These consisted of hour-long following episodes in which we recorded social behaviors, including pant grunts and aggression. These focal samples were distinct from and in addition to "contact time" hours of observation. A.A.S. followed chimpanzees during 431 h of focal observations between August 2014 and August 2015. Focal following episodes included observations of three middle adolescents and seven late adolescents (total hours/individual ± SD: 43.1 ± 3.1 h). R.B.R. followed males during 155 focal hours between June and August 2015. Subjects included 9 early adolescents, 4 middle adolescents, and 7 late adolescents (total hours/individual ± SD: 7.7 ± 2.2 h; Online Resource 1). During 2 months, A.A.S and R.B.R. conducted observations concurrently, and for the most part, independently. A few times, however, they observed the same subject simultaneously. This created some overlap in contact time and focal hours of observation, leading to a slight overestimate in total hours of observation. Nevertheless, we guarded against the possibility of inflating our behavioral observations of pant grunts and aggressive acts by carefully reviewing our data and counting cases in which both observers recorded the same pant grunt or aggressive act only once.

Statistical analyses

We tallied all instances of pant grunts and aggression given to and received by other adolescents. We entered these values into two separate interaction matrices, one for pant grunts (Table 2) and another for aggression (Table 3). To assess whether adolescents form a linear dominance hierarchy, we calculated de Vries (1995) improved test of linearity (h'), which is based on Landau's h, using DomiCalc (Schmid and de Vries 2013) in Microsoft Excel. This measure of linearity ranges from 0, indicating a non-linear hierarchy, to 1, indicating a completely linear, or transitive hierarchy (de Vries 1995; Schmid and de Vries 2013). To assess significance, we performed 10,000 randomizations of the linearity test, which generated a random linearity index, h_r. We compared h_r to the test statistic, h_O, which is equivalent to h', the unbiased estimate for Landau's h (Schmid and de Vries 2013). If the probability of $h_r \geq h_O$ is less than 0.05, the hierarchy is considered significantly linear. More details regarding the calculation of h' and the test of linearity can be found in the handbook for DomiCalc (V. S. Schmid) (Schmid and de Vries 2013).

Table 2 Pant grunt matrix for adolescent males

	Caller age	16.1	16.1	15.4	15.2	15.2	15.1	14.7	14.1	14.0	13.1	12.8	12.1	10.3	10.1	10.1	10.1	10.1	9.1	9.1	9.0	8.7	8.6	8.6	
Recipient age		Haden	Mitchell	Lovano	Abrams	Wilson	Buckner	Benny	Chopin	Barron	Erroll	Booker	Bosko	Murray	BillyBragg	Elton	Jarman	Orff	Powell	YoYo	PeeWee	Fleck	Damien	Dylan	Sum pant grunts received
16.1	Haden	*	0	0	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	(0)	0	0	**1**	0	1
16.1	Mitchell	0	*	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	**1**	(0)	0	**1**	0	(0)	0	2
15.4	Lovano	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.2	Abrams	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1
15.2	Wilson	0	0	0	**1**	*	0	0	0	**2**	**1**	0	0	0	0	0	0	0	0	0	**4**	0	0	0	8
15.1	Buckner	0	0	0	0	0	*	0	0	0	0	0	0	**2**	**3**	0	0	0	(0)	0	0	0	**1**	0	6
14.7	Benny	0	0	0	0	0	0	*	0	0	0	0	0	0	**1**	(0)	**1**	0	(0)	0	0	0	0	0	2
14.1	Chopin	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0
14.0	Barron	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1
13.1	Erroll	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12.8	Booker	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0
12.1	Bosko	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	(0)	0	0	0	(0)	0	0
10.3	Murray	0	(0)	0	0	0	0	0	0	0	0	0	0	*	0	(0)	0	0	(0)	0	0	0	0	0	0
10.1	BillyBragg	(0)	0	0	0	0	0	0	0	0	0	0	0	0	*	(0)	0	0	(0)	0	0	0	0	0	0
10.1	Elton	0	0	0	0	0	0	(0)	0	0	0	0	0	(0)	(0)	*	0	0	0	0	0	0	(0)	0	0
10.1	Jarman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0
10.1	Orff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0
9.1	Powell	0	(0)	0	0	0	(0)	(0)	0	0	0	0	(0)	(0)	(0)	0	0	0	*	(0)	0	0	0	0	0
9.1	YoYo	(0)	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	(0)	*	0	0	0	0	0
9.0	PeeWee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0
8.7	Fleck	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0
8.6	Damien	0	(0)	0	0	0	0	0	0	0	0	0	(0)	0	0	(0)	0	0	0	0	0	0	*	0	0
8.6	Dylan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Sum pant grunts given		0	0	0	1	0	0	0	0	2	1	0	0	2	4	0	1	1	0	0	5	0	2	2	

Individuals are ordered by age (years); ages reported in the Table are based on age at the midpoint of study (February 1, 2015); pant grunts are shaded; zeros in parentheses indicate individuals that were never observed in the same subgroup and thus had no opportunity to interact; dashed line separates late adolescents from middle and early adolescents; solid line separates males who some researchers would consider adults (15 years and older)

Table 3 Aggression matrix for adolescent males

	Recipient age	16.1	16.1	15.4	15.2	15.2	15.1	14.7	14.1	14.0	13.1	12.8	12.1	10.3	10.1	10.1	10.1	10.1	9.1	9.1	9.0	8.7	8.6	8.6	
Aggressor age		Haden	Mitchell	Lovano	Abrams	Wilson	Buckner	Benny	Chopin	Barron	Erroll	Booker	Bosko	Murray	BillyBragg	Elton	Jarman	Orff	Powell	YoYo	PeeWee	Fleck	Damien	Dylan	Sum aggression given
16.1	Haden	*	0	0	0	0	0	0	0	1	2	2	0	0	(0)	0	0	0	0	(0)	3	1	1	0	10
16.1	Mitchell	0	*	0	0	0	0	0	1	1	0	0	1	(0)	0	0	0	0	(0)	0	0	0	(0)	0	3
15.4	Lovano	1	0	*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
15.2	Abrams	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
15.2	Wilson	2	0	2	1	*	0	0	1	1	2	2	0	0	0	0	1	0	0	0	5	0	1	1	19
15.1	Buckner	0	0	0	0	0	*	0	0	0	0	0	0	1	2	0	0	0	(0)	0	0	0	0	0	3
14.7	Benny	0	0	0	0	0	0	*	0	1	0	0	0	1	2	(0)	0	0	(0)	0	0	0	0	0	4
14.1	Chopin	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0
14.0	Barron	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
13.1	Erroll	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	1	0	0	1	0	1	0	3
12.8	Booker	0	0	0	0	0	0	0	0	0	1	*	0	0	0	0	0	0	0	0	0	0	1	0	2
12.1	Bosko	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	(0)	0	0	0	(0)	0	0
10.3	Murray	0	(0)	0	0	0	0	0	0	0	0	0	0	*	1	(0)	0	0	(0)	0	0	0	0	0	1
10.1	BillyBragg	(0)	0	0	0	0	0	0	0	0	0	0	0	0	*	(0)	0	0	(0)	0	0	0	0	0	0
10.1	Elton	0	0	0	0	0	0	(0)	0	0	0	0	0	(0)	(0)	*	0	0	0	0	0	0	(0)	1	1
10.1	Jarman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0
10.1	Orff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0
9.1	Powell	0	(0)	0	0	0	(0)	(0)	0	0	0	0	(0)	(0)	(0)	0	0	0	*	(0)	0	0	0	0	0
9.1	YoYo	(0)	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	(0)	*	0	0	0	0	0
9.0	PeeWee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	1	0	1
8.7	Fleck	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0
8.6	Damien	0	(0)	0	0	0	0	0	0	0	0	0	(0)	0	0	(0)	0	0	0	0	0	0	*	0	0
8.6	Dylan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Sum aggression received		3	0	2	1	1	0	0	2	4	5	4	1	2	5	0	1	2	0	0	9	1	5	3	

Individuals are ordered by age (years); ages reported in the Table are based on age at the midpoint of study (February 1, 2015); aggressive events are shaded; zeros in parentheses indicate individuals that were never observed in the same subgroup and thus had no opportunity to interact; solid line separates males who some researchers would consider adults (15 years and older)

Results

We recorded 857 pant grunts between males of all ages. Only 21 (2.5 %) of these were exchanged between adolescent males. Most pant grunts were given by adolescent males to adults ($N = 569$). Adolescent male chimpanzees received very few pant grunts. Early adolescents (8–10 years old, $N = 11$) and middle adolescents (11–13 years old, $N = 5$) never received pant grunts (Fig. 1a). Six of the seven late adolescents (14–16 years old) received pant grunts from 1 to 4 individuals, and these tended to be pant grunts from much younger adolescent males (mean difference in age ± SD = 4.8 ± 2.02 years younger; range = 7.4 younger to 0 years older; Fig. 1a). Based on pant grunts, only 5.5 % of adolescent male dyads had decided relationships (14/253 dyads). There was no indication of a linear hierarchy ($h' = 0.132$; $P = 0.458$). These results contrast with the pattern between adults. Although adult males were not the focus of our study, we recorded 265 pant grunts between adult males 17 years and older. Only 24 % of all adult male dyads exhibited decided relationships (104/435), but there was a linear hierarchy ($h' = 0.221$; $P = 0.002$).

One late adolescent, Abrams (15.5 years old) received a pant grunt from a low-ranking young adult male (Hawkins, 20.5 years old). This was the only time that an adolescent male received a pant grunt from an older chimpanzee. The dominance relationship between Abrams and Hawkins appeared to be in flux, as Abrams had pant grunted to Hawkins earlier in the year. Adolescent males who belonged to the same age-class exchanged pant grunts 2 times. Both cases involved one late adolescent (Wilson, 15.5 years old), who received pant grunts from two other late adolescents (Abrams, 15.5 years old and Barron, 14.3 years old). All other pant grunts received by late adolescents were given by males who were early adolescents or, on one occasion, a middle adolescent (Table 2). Half of the adolescent males ($N = 13$) were never observed pant grunting to other adolescents (Table 2). In sum, male chimpanzees did not receive pant grunts until late adolescence.

Like pant grunts, aggressive interactions between adolescent males were also rare, accounting for 10 % of all aggressive acts observed between male chimpanzees of all ages. We recorded 502 cases of male–male aggression but only recorded adolescent males behaving aggressively with each other 51 times. Most of these cases involved non-contact aggression (47/51 times), including displays, charges, and chases. We recorded contact aggression, involving hitting, slapping, and kicking, only 4 times. Based on aggression, only 14.2 % of dyads had decided relationships (36/253 dyads), and there was no linear hierarchy ($h' = 0.163$, $P = 0.247$). Combining aggression and pant grunts into one matrix produced similar results. Only 16.2 % of all adolescent male dyads exhibited decided relationships (41/253), and there was no evidence of a linear hierarchy ($h' = 0.175$, $P = 0.186$).

Early adolescent males directed aggression toward other adolescents only 3 times (Fig. 1b; Table 3). One event involved charging, and two involved one male shaking branches at another. Early adolescent males were victims in all three cases. Middle adolescents were aggressors 6 times. A middle adolescent charged another middle adolescent once. The five other occasions involved a middle

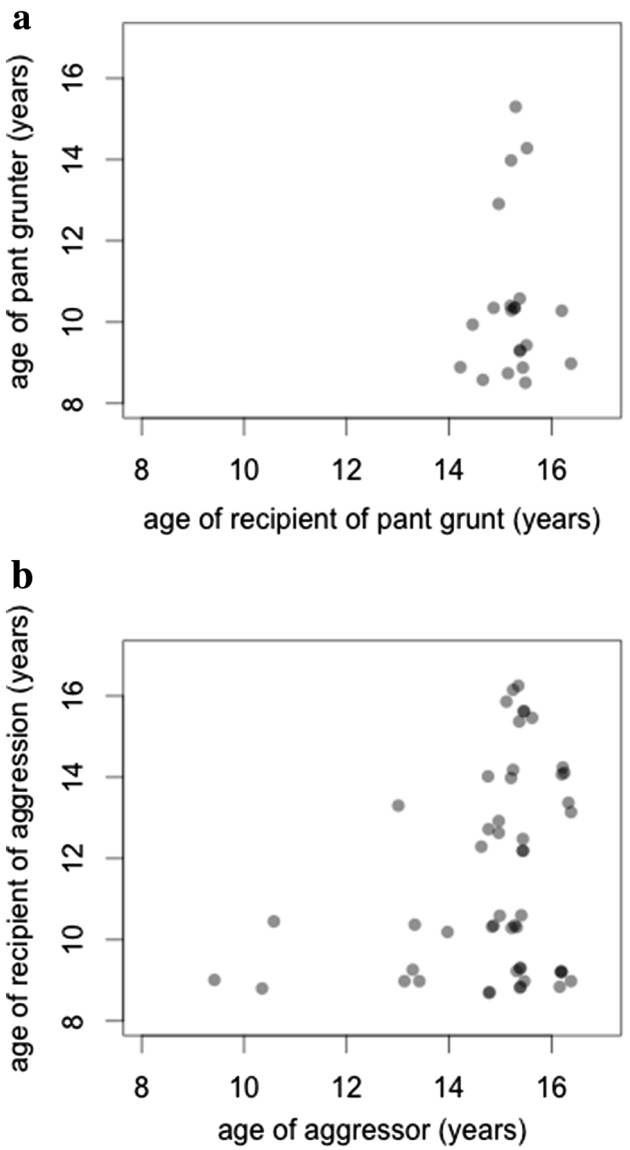

Fig. 1 Dominance rank interactions between adolescent male chimpanzees (8–16 years old). **a** Pant grunts. The age of callers (subordinate individuals) is plotted vs the age of recipients (dominant individuals). **b** The age of recipients of aggression (subordinate individuals) is plotted vs the age of aggressors (dominant individuals). Interactions between males of different ages are denoted by semi-transparent *gray dots*, with *darker dots* representing overlaid data points, e.g., the dot at (15.3, 10.4) in 1a appears dark because 10.4-year-old males pant-grunted to 15.3-year-old individuals multiple times

adolescent behaving aggressively toward an early adolescent. One of the latter events resulted in contact aggression when Erroll (age 13.3 years) hit Orff (age 10.4 years) with a branch after Orff interrupted Erroll mating with an adolescent female. The remaining 42 cases of aggression involved late adolescents as aggressors. Seventeen of these aggressive events were single acts of aggression, but four late adolescents engaged in aggression more than once with the same adolescent. These involved ten dyads in 24 acts. Aggression was unidirectional across dyads, with one exception. Wilson, a late adolescent, charged and displayed at Lovano, another late adolescent, once. Lovano chased Wilson another time.

Adolescents tended to direct aggression toward individuals who were younger than themselves (mean difference in age ± SD = 3.35 ± 2.52 years younger; range = 7.4 years younger to 0.9 years older). These acts exclude cases where adolescent males behaved aggressively toward adult males, which occurred 13 times. One of these instances involved a middle adolescent, Booker (age 13.1 years) displaying at a very small, low-ranking, and old adult male (Dizzy). All other instances involved late adolescents, including five individuals whose mean age was 14.9 years. Wilson accounted for five of these aggressive acts, and Abrams was the aggressor 4 times. The recipients of aggression were either young adults or very low ranking adult males, including two individuals with chronic injuries due to snares.

Discussion

Given the absence of pant grunts received by early and middle adolescents, the paucity of pant grunts exchanged between late adolescents, the infrequent occurrence of adolescent-to-adolescent aggression, and the absence of a linear dominance hierarchy, it is reasonable to conclude that adolescent male chimpanzees at Ngogo do not display decided dominance relationships. These findings contrast with the patterns displayed between adult males, who pant grunted to each other more often than did adolescent males and who, unlike adolescents, formed a linear dominance hierarchy.

Aggressive interactions between adolescents occurred more often than the exchange of pant grunts, but were nonetheless still relatively rare. Most aggressive acts were given by late adolescents to early adolescents. Only at age 15 years did some males begin to dominate other adolescents to whom they were close in age. This is the same time that male chimpanzees typically attempt to integrate themselves into the adult male dominance hierarchy by starting to behave aggressively toward low-ranking adult males (Pusey 1990; Nishida 2012).

Most pant grunts (17/21 = 81 %) were given to males who were 15 and 16 years old. We were liberal in classifying these males as adolescents following precedents set earlier by Goodall (1983) and Sherrow (2008, 2012). Nevertheless, the possibility exists that these individuals had crossed the threshold to adulthood, as other chimpanzee researchers consider them to have done so (Muller and Wrangham 2004a). But if we adopted the criterion

employed by some, an age cut-off of 14 years old and younger to define adolescence (Nishida 1997; Muller and Wrangham 2004a), we would have recorded even fewer pant grunt exchanges between adolescent males: only 4 times. Taken together, these observations indicate that adolescent males at Ngogo, like adolescent male chimpanzees elsewhere, do not form decided dominance relationships with their male peers.

Adolescent male chimpanzees pant grunt to one another at Gombe and Mahale only very rarely or not at all (Bygott 1979; Hayaki et al. 1989). These findings and our own, differ from Sherrow's (2012) previous observations at Ngogo. Sherrow (2012) reported that adolescent males there display decided dominance relationships and form a linear dominance hierarchy. Sherrow recorded 99 pant grunts between adolescents during 15 months of study between 2000 and 2004. This count far exceeds the 21 calls we observed in 12 months of study between 2014 and 2015. These observations leave us with an obvious and unresolved question: what explains these different findings?

As noted in the Introduction, there were pronounced differences in the way the ages of male subjects were determined in this study and in Sherrow's (2008, 2012) earlier work, and this likely contributed to our discrepant findings. Sherrow began his research only 5 years after long-term observations commenced at Ngogo. At that time, the adolescent males were difficult to observe on the ground, and their ages were estimated using their physical appearance and behavior (Sherrow 2008). Over the past 15 years, the ages of all individuals have been reassessed using pedigree and genetic data and observations of the developmental trajectories of males of known ages (Wood et al. 2016). Using these revised estimates, nine of Sherrow's 17 subjects were likely to have been young adults, 17 years old and older, rather than adolescents during the majority of his study. In contrast, our male subjects were first observed as infants and juveniles, and their ages can be estimated to the nearest month or year. While it is impossible to know with certainty the ages of the young males observed by Sherrow, we can say with confidence that the adolescents we observed were adolescents and that they do not form a dominance hierarchy with their peers.

Our observations that late adolescent males receive pant grunts and give aggression more often than do younger males are suggestive of an age-based hierarchy. While this possibility exists, it is impossible to evaluate in the absence of additional data on dominance interactions between adolescent males. The paucity of data in this regard may be due to the fact that we followed early adolescent males as focal subjects over a relatively short period and only a few times (56 focal hours over 3 months). The results that we have reported here should be considered with this in mind. We did have considerable contact time with early adolescents (732 h over 12 months by A.A.S. and 307 h over 3 months by R.B.R), but our ad libitum observations may have missed instances of aggression involving them. Nevertheless, the fact remains that we observed adolescent males pant grunting to other adolescent males only a very few times. In addition, our observations of an extremely large cohort of middle and late adolescent males provide no hint of an adult-like hierarchy among the older adolescents.

Another issue that we did not address specifically involves variation in opportunities for adolescents to interact. Given the fission–fusion nature of chimpanzee communities, some individuals associate more than others (Nishida 1968; Goodall 1986; Newton-Fisher 1999; Pepper et al. 1999; Mitani and Amsler 2003). This is especially true of adolescents, who do not range as widely within the territory as do adult males. In the present analysis, we did not account for "structural zeros," or the absence of dominance interactions due to a lack of opportunities to interact (de Vries 1995). We do not suspect that an absence of opportunities influenced our results, as most adolescent males had ample chances to exchange calls and engage in aggression. The majority of dyads (236/253) associated with one another, but males in these pairs rarely pant grunted to each other, and clear dominance relationships between them were impossible to discern. Given this, the formal analysis of linearity that we performed (de Vries 1995; Schmid and de Vries 2013) yielded a predictable null result and provides a stark contrast to the findings from the previous study at Ngogo (Sherrow 2012). In sum, further investigation of early and middle adolescent aggressive behavior and dominance relationships is required. Until then, the preponderance of current evidence indicates that adolescent male chimpanzees do not form a dominance hierarchy with their peers.

The finding that adolescent male chimpanzees do not establish decided dominance relationships between themselves may be surprising given the importance of rank in adulthood and the fact that other primates form dominance relationships during adolescence. Why do male chimpanzees wait until adulthood? The prolonged time it takes male chimpanzees to form dominance relationships with others in their community represents one possibility. Male chimpanzees begin the process of establishing rank by behaving aggressively toward and attempting to dominate adult females (Pusey 1990; Nishida 2003). This takes time and involves nontrivial effort because adult females retaliate with aggression and are able to rebuff their challenges, at least initially (Pusey 1990; Nishida 2012). As a consequence, male chimpanzees are able to achieve dominance over adult females only toward the end of adolescence (Goodall 1986; Pusey 1990). They then start to compete with their peers, but by this time, they have already crossed the threshold to adulthood.

Adult male behavior is a second factor that might limit and constrain aggression and competition between adolescent male chimpanzees. Here, adolescent males may avoid aggression with peers as this can lead to retaliation by adults. Although we did not quantify it, on some occasions higher-ranking adults attacked adolescent and young adult males after the latter behaved aggressively. Consequently, adolescents may benefit by remaining under the radar of adult males. It is only after they have reached physical and social maturity in adulthood that male chimpanzees are able to compete effectively with conspecifics, and this may be the time that they switch gears and start to strive for status and attempt to dominate their peers.

A third possibility is that adolescent males prioritize forming social bonds over competing with each other. Male chimpanzees are philopatric, and to reproduce they must integrate themselves into the social network of adult males. Consequently, their effort might be better spent on developing affiliative rather than agonistic relationships with peers, as cooperative bonds in adulthood translate into fitness benefits (Watts and Mitani 2001; Mitani 2009; Gilby et al. 2013). To date, few studies have investigated the development of social bonds in adolescent male chimpanzees (Kawanaka 1989, 1993; Pusey 1990). Whether adolescents form social bonds with their peers remains an open question and requires additional research.

Although adolescent male chimpanzees do not vie for status with their peers, aggressive encounters between adolescents may still be important for future dominance relations. Juveniles and early adolescents engage in aggressive interactions occasionally (Markham et al. 2015), and in captivity, adolescents display dominance in the context of play (Paquette 1994). Although distinct from adult dominance relationships, juvenile play may be important practice and have an impact later in adulthood. For example, juvenile marmot play patterns predicted adult dominance relationships (Blumstein et al. 2013). Given that it takes male chimpanzees a long time to grow up, the social behaviors exhibited during juvenility and adolescence may have important consequences in adult life.

In sum, our finding that adolescent male chimpanzees do not establish dominance relationships with their peers is surprising given the importance of rank in adult male chimpanzee life. It is also perplexing because dominance appears to manifest during adolescence in other primates, including humans (Savin-Williams 1979; Pellegrini 2002). The three hypotheses that we have proposed above require testing. Given the fundamental importance of understanding the development of behavior (Tinbergen 1963), these tests, along with additional studies of chimpanzee adolescence and ontogeny, remain a high priority for future research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Statement of human and animal rights All applicable international and institutional guidelines for the care and use of animals were followed.

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